

SEEDS AND FRUIT OF THE GOODENIACEAE

R. C. CAROLIN

University of Sydney

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Synopsis

The microscopic structure of the seeds and fruits of the Goodeniaceae is examined. In general, the results are found to correlate with those in previous papers by Carolin and Peacock. Changes in the classifications proposed by previous authors are suggested. A new interpretation of the ovary of *Scaevola* is suggested. Seven seed types are recognized in *Goodenia* and its satellite genera, characterized by the relative position, size, and shape of the thickened (cells) and the mucilage cells of the epidermis of the testa. Eight pseudo-fruit types of *Scaevola* are recognized, based on the constitution of the three "layers" in the wall.

INTRODUCTION

Seeds and fruits play a prominent role in the classification of the Angiosperms and it is frequently instructive to re-evaluate their characters within a group.

The form of the fruits together with ovule number of the Goodeniaceae have been used to characterize the genera (Krause, 1912) and even to divide it into new families (Lindley, 1836). Their structure has also been used to distinguish between the species of *Goodenia* and *Velleia*, notably with regard to the presence or absence of a wing. No-one, however, has examined the seed structure at the microscopic level. Neither has anyone made any comparison of the seed types of this family and its supposed relations.

MATERIALS AND METHODS

In general, the seeds were collected from herbarium specimens, either made especially for the purpose or collected by other workers. Freshly collected seeds were sometimes used. Observations on the fruits were also made largely from herbarium specimens and sometimes in the field. All voucher specimens are cited separately. Herbarium abbreviations are those given in "Index Herbariorum", ed. 5.

Transverse sections of individual seeds were cut, although generally sections of the endocarp were also included in the case of drupaceous fruits. The testa or endocarp was usually so tough that it had to be softened in 20% nitric acid for periods of up to two months. Sections were cut on a sledge microtome at 20 μ without embedding or after embedding in collodion using amyl acetate as the solvent and the "dry" method (Steedman, 1960).

The vasculature of the seeds was observed in whole mounts of (usually) slightly immature seeds. Those embedded in an endocarp were extracted and those which required it were bleached in a commercial chlorine bleaching agent. They were then cleared and examined in Chloral-hydrate-lactophenol (CLP, Bersier and Bocquet, 1960).

The ratio a:b (radicle width : cotyledon width) was measured by a graticule in a binocular stereoscopic-microscope with a $\times 40$ magnification.

OBSERVATIONS

The food-store of the Goodeniaceae was not examined in such detail as the characteristics outlined below. Starch was not detected in any of the seeds examined below, through using polarized light. The following species

(all those examined) failed to show any blue coloration with iodine: *Goodenia bellidifolia*, *G. stelligera*, *G. ovata*, *G. mitchellii*, *Dampiera stricta*, *Scaevola albida*, *S. calendulacea*, *Velleia paradoxa*, *Brunonia australis*. None of these species gave a reaction to Hotchkiss' test for polysaccharides (Glick, 1949) except in the relatively thin cell walls. All showed the presence of oil using the Sudan III test. All of them also contained large numbers of aleurone grains which gave a weak reaction to Millons test (Glick, 1949). It seems, then, that food-store in the seed consists almost exclusively of oils and proteins.

BRUNONIA

This genus differs from all the others in the family in having a very reduced endosperm. The seed storage-tissue is contained in the two massive cotyledons, at the base of which is the minute embryo.

The single seed is uncompressed and contained in a membranous pericarp, itself surrounded by the broken, membranous remains of the corolla and the thickened calyx. The latter is the main dispersal unit as the tube and spreading lobes are conspicuously hairy.

The seed has a single vascular strand which extends partly down the micopylar side of the organ. The seed coat is thin and most of the internal walls of the testa are broken; there is apparently no thickening of the epidermis, although the highly refractive cuticle is fairly conspicuous. The brownish colour of the seed is due to the discoloured broken down inner regions of the integument which occupies a very narrow band immediately inside the testa. Just inside from this is a single layer of cells, apparently alive, but probably not functional, which represent the remains of the endosperm (Fig. 2, E, F). The bulk of the seed is taken up by the cotyledons.

There appears to be no differentiation of the epidermal cells as found in *Goodenia*, etc., and the epidermis does not seem to be mucilaginous in any way.

LESCHENAULTIA

The fruits of this genus are described as capsules dehiscing through four valves. This is partly incorrect. $a:b=1$, embryo terete in all species.

In *L. biloba* the four sepaline ribs (two sepals are connate in this region) separate from the inner parts followed, almost immediately, by the four semi-free corolla parts (see Carolin, 1959) thus giving eight valves in all, four large ones and four small ones. The inner parts of the fruit are hard and woody. Moreover, during the development of the fruit, the outer walls of the loculi, particularly where these are free from the outer whorls, i.e., opposite four petal radius traces (Carolin, 1959), have grown inwards and partially fused, with smaller outgrowths from the axile placenta. The result is that the seeds are entirely surrounded by tissue derived from the loculus wall. As development proceeds the tissue between each seed separates horizontally (Fig. 1, A-D) thus forming an "article" containing the seed. Further growth causes the individual articles to separate from each other (Fig. 1, A). It is these units which, in the past, have been referred to as seeds: the so-called "testa" (Bentham, 1869, etc.) is really the inner layers of the pseudo-fruit, the cells of which have very greatly thickened walls (Fig. 1, F, G). The testa itself is a very inconspicuous, thin-walled layer, in some species showing narrow bands of thickening in the epidermis (Fig. 1, E). It seems probable that the thickened layers are homologous with the true fruit, since all the cells inside the closed "spurs" (Carolin, 1959) have thickened walls. It is implied, then, that the outer floral parts separate from the fruit and then the fruit breaks, like a lomentum, into a double series of articles (Fig. 1, A). The thickened layers of the fruit, whilst being fairly well-defined from the outer thin-walled cells,

are not bounded by a definite differentiated layer as in *Dampiera*. The shape of these articles is frequently a specific characteristic; *L. linarioides*, *L. longiloba*, and *L. filiformis* share the same significant features.

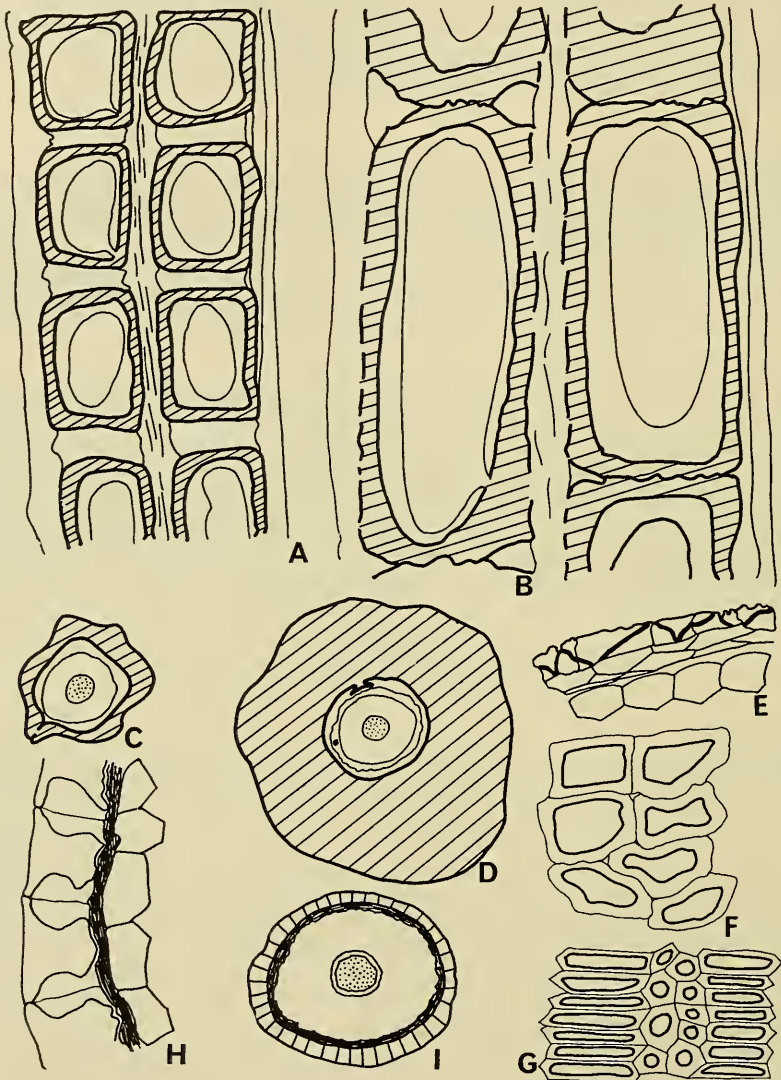


Fig. 1. A. longitudinal section of part of fruit of *Leschenaultia biloba* $\times 8$; B. same of *L. linarioides* $\times 8$; C. transverse section of pyrene, *L. filiformis* $\times 20$; D. transverse section of pyrene, *L. divaricata* $\times 12$ large stippling = dry soft tissue; hatching = hard tissue; E. epidermis of seed, *L. biloba* $\times 320$; F. cells from pyrene wall, *L. biloba* $\times 160$; G. cells from pyrene wall, *L. divaricata* $\times 160$.

L. divaricata shows some differences from the other species examined. No material was available for observation of the development of the fruit. The mature fruit, however, shows only a single seed developed at any one level and a cross-section shows that the article is derived from both loculi. The swelling of the seed has ruptured the septum (Fig. 1, D) and there is no

division along the placenta when the fruit breaks up, as there is in the other species. Moreover, the thickened cells of the article are more regularly arranged than in the other species (Fig. 1, G).

The seed itself seems to be fairly uniform in the genus. The vasculature is quite reduced, consisting of a single strand which scarcely reaches the top of the somewhat elongated, more or less terete seed (Fig. 3, D). The epidermis

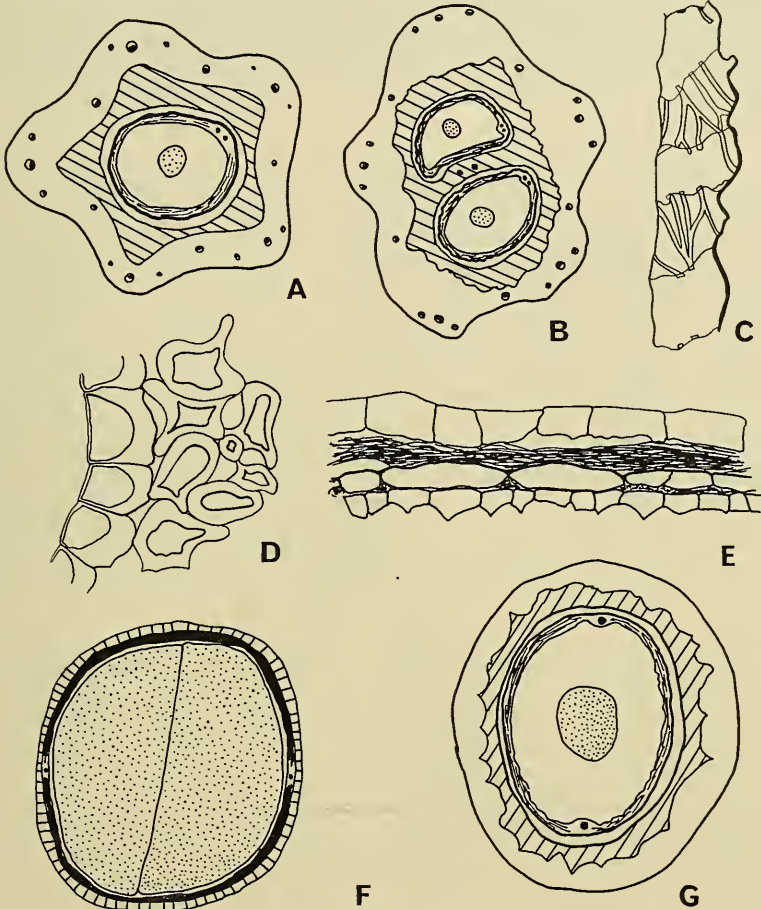


Fig. 2. A. transverse section of fruit, *Dampiera stricta* $\times 20$; B. transverse section of fruit *D. trigona* $\times 20$; C. epidermis of seed, *D. stricta* $\times 320$; D. cells of pyrene wall, *D. stricta* $\times 320$; E. seed epidermis, etc., *Brunonia australis* $\times 320$; F. transverse section of seed, *B. australis* $\times 20$; G. transverse section of fruit of *Diaspasis filiformis* $\times 20$, e=epidermis, en=endodermis, c=cotyledon: stipple=embryo, diagonal hatching=hard tissue.

of the testa is very narrow and is only thickened, if at all, by lignin bands similar to those of *Dampiera*. Indeed the seed resembles that of *Dampiera* sect.(eu)-*Dampiera* quite closely, although it is smaller, smooth, and has a reduced vascular system.

DAMPIERA

Embryo terete, a:b=1:1 in all species. The two forms of ovary (2-locular and 1-locular) are reflected in the fruit form (Fig. 2, A, B). But apart from the number of loculi there is no significant difference between seed and fruit of *D. trigona* in sect. *Dicoelia* and *D. stricta* and the rest of the

"*eu-Dampiera*". The fruit is divisible into a hard, woody inner layer with thickened cell-walls and a relatively soft but scarcely fleshy and never very thick outer layer. There seems, in general, to be little change in this latter layer as the ovary matures into a fruit; there is no visible increase in fleshiness. One cannot, strictly, equate these layers with endo- and meso-carp of a drupe as the "fruit" is a pseudo-fruit and not strictly equivalent to a drupe, a true fruit. Indeed, it seems probable that the hard inner layer is ovary and the soft outer layer the adnate outer whorls, although evidence for this would be hard to gather. The hard inner layer may be rugose or wrinkled as in *D. trigona* and *D. stricta*, or almost smooth as in *D. coronata*. The outer surface of the endocarp is delimited by a specialized group of often somewhat enlarged

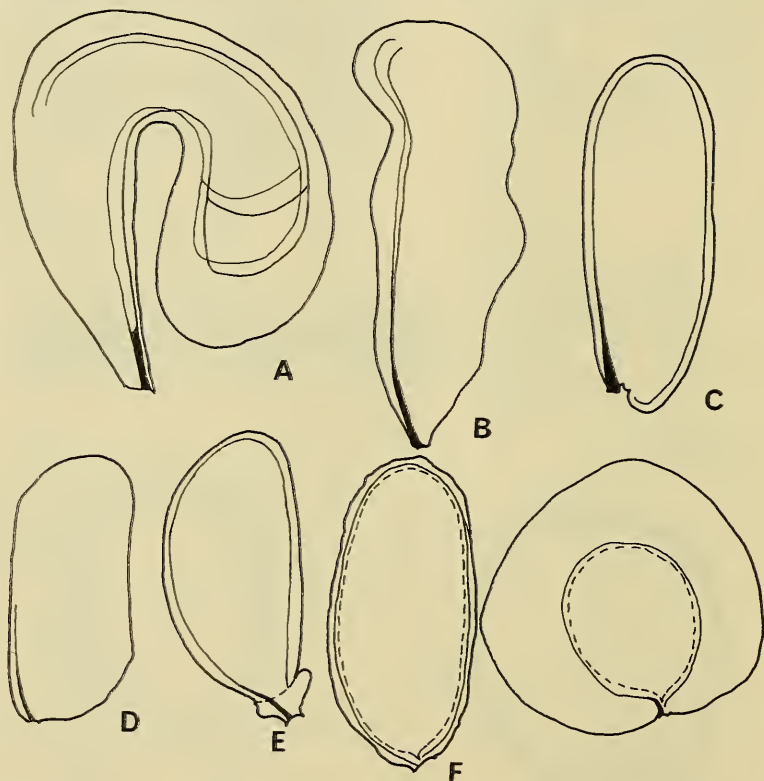


Fig. 3. Diagrams of cleared seeds showing vascular patterns; broken lines=edge of wing. A. *Dampiera coronata*; B. *D. purpurea*; C. *Scaevola calendulacea*; D. *Leschenaultia biloba*; E. *Goodenia barbata*; F. *G. heterophylla*; G. *Velleia connata*.

cells. These are more or less regularly arranged inside a zone of loosely arranged aerenchyma. The inner tangential and radial walls of this layer become thickened with a refractive substance which does not stain with normal lignin stains (safranin, gentian violet). Thus the limit of the pseudo-endocarp is quite clear. Inside this layer the parenchyma is heavily thickened with lignin (Fig. 2, B).

The seeds themselves usually follow the outline of the pseudo-endocarp; thus, those with corrugated "endocarp" have corrugated seeds and those with smooth "endocarp" a smooth seed. The testa is thin and delicate and is probably always slightly thickened with reticulate bands of lignin when quite mature. These, however, were only actually observed on *D. stricta*. The inner integument zones are, likewise, very thin-walled and consequently quite crushed in the mature condition.

All the seeds examined show a double vascular supply almost to the base, two strands diverging from the funicle, e.g. *D. stricta*, *D. trigona*, although both strands remain on the same side of the seed. In *D. purpurea* they remain very close together and appear to be single for almost half the length of the seed. These vascular strands normally end at the top of the seed (Fig. 3, B).

The sect. *Camptospora* is distinguished by the peculiar bent seed. The general structure is the same but the vascular supply, whilst recognizably based on the same pattern, is more developed. The main strands are longer, reaching almost to the base, and there are distinct and constant secondary, connecting strands (Fig. 3, A).

ANTHOTIUM

Embryo terete, $a : b = 1 : 1$. *A. rubriflorum* only examined. The seeds are small (c. 1 mm. long) and black. The vascular strand is single and very short indeed. The transverse section shows the small \pm terete embryo embedded in endosperm, the crushed brownish inner parts of the integuments, and the outer epidermis of the integument (Fig. 1, I). This latter has much thickened radial walls, which are black, but both tangential walls are thin and, indeed, the uppermost is usually collapsed inwards until the seed is placed in water. Thus the dry seed is alveolate on the surface but, when placed in water, the dry cell contents swell up, force the upper epidermis outwards, occasionally even rupturing it. This does not seem to be "mucilage" in the same sense as applied to the epidermis of *Goodenia*. There is none of the characteristic disc-like stratification within the cells; it takes much longer to swell up and there is no reaction with iodine (Fig. 1, H).

The cells of the epidermis appear to be all of the same type. There is no differentiation between thickened and mucilage cells.

DIASPASIS

D. filiformis is the only species. The false-fruit is differentiated into an inner, rugose, layer of cells with much thickened walls and an outer layer which is not particularly fleshy but consists largely of parenchymatous cells. The boundary of the two layers is quite clearly marked but the outermost thickened cells are not significantly different from the others (unlike *Dampiera*).

The seed is \pm ovoid in shape. There appears to be generally only one developed, the other ovule aborting, its loculus compressed and the septum frequently ruptured with the growth of the seed. The seed has a single vascular strand which continues almost to the micropyle (cf. *Scaevola*). The epidermis cells are only thickened with lignin bands (as in *Dampiera*); in no case is the thickening general. Moreover, there seems to be no differentiation of the epidermis above the vascular strand (as in *Goodenia*), except that these cells are more isolateral than the horizontally elongated cells elsewhere in the epidermis. The inner layers of the integument are crushed against the epidermis by the massive endosperm (Fig. 2, G). The central embryo is terete to very slightly spatulate.

GOODENIA (see Fig. 10)

Of all the genera in the family, *Goodenia* shows the greatest variation in seed morphology. In transverse section, seven different forms can be distinguished. The first one, as described below, is quite distinct and shows little relationship with the others. The next six, on the other hand, intergrade with one another. In all the species included to date within this genus, the fruit is capsular. The seed in all cases shows a single, unbranched vascular strand which extends from the funicle around to the micropyle (Fig. 3, E, F).

Type 1

Embryo terete, $a:b=1:1$. The seed here is ovoid and, in transverse section, is more or less circular in outline. The epidermis of the testa is palisade-like, i.e., elongated radially, and the cell-walls are much thickened with prominent pits but more or less straight sides (Fig. 4, B), not convoluted as in other types. The outer tangential wall is usually somewhat less thickened than the radial. All the epidermal cells have more or less the same form; there are no mucilage cells. The inner parts of the integument are crushed

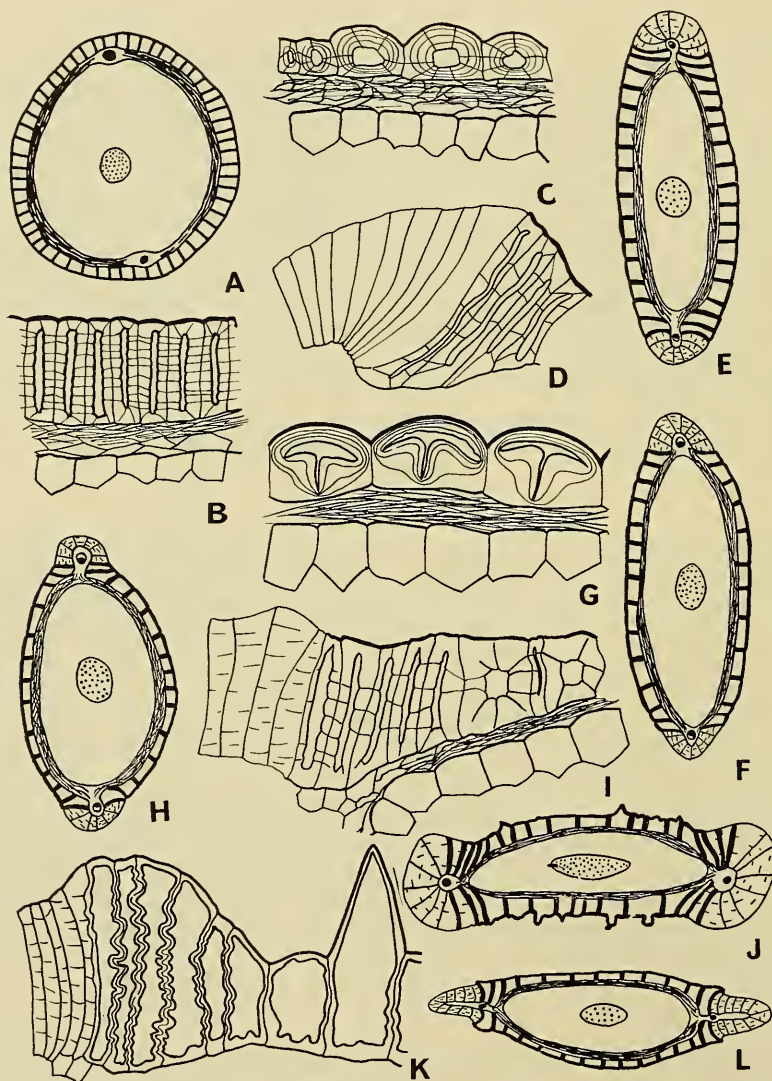


Fig. 4. Transverse sections of seeds. A. *Goodenia barbata* $\times 20$; B. *G. barbata*, epidermis $\times 160$; C. *G. ovata*, epidermis from middle of seed face $\times 160$; D. *G. ovata*, epidermis from margin $\times 160$; E. *G. ovata* $\times 20$; F. *G. azurea* $\times 20$; G. *G. azurea*, epidermis $\times 160$; H. *G. paniculata* $\times 20$; I. *G. paniculata*, marginal epidermis $\times 160$; J. *G. glabra* $\times 20$; K. *G. glabra*, marginal epidermis $\times 160$; L. *G. stelligera* $\times 20$.

against the epidermis by the massive endosperm, in the centre of which is the terete embryo (Fig. 4, A). The upper part of the funicle is swollen into a small strophiole, e.g. *G. barbata*, *G. strophiolata*, *G. chisholmii*.

In all the other types there is differentiation within the epidermis of the more or less compressed seed. The epidermal cells on the surface have much thickened walls, whilst those towards the margin have very thin walls and are generally filled with a mucilage which swells up and bursts through the outer-tangential wall on wetting and stains a deep blue with iodine. The vascular strand runs in a canal of uncrushed integument tissue just below these mucilaginous cells.

Type 2. (a)

Embryo slightly spathulate, $a : b = 2 : 3$ (*G. ovata*, etc.), $1 : 1$ (*G. paniculata*). The thickened cell walls in the epidermis are hardly convoluted, except those close to the mucilage cells and then not very much so; mostly the cells are \pm isolateral. The mucilage cells do not overlap the thickened cells a great deal, if at all, neither do the thickened cells arch over the mucilage cells. The margin is thus quite rounded without any secondary rims (Fig. 4, C-I), e.g., *G. ovata*, *G. paniculata*.

Type 2. (b)

Embryo slightly spathulate, $a : b = 2 : 3$ or $2 : 2\frac{1}{2}$. Intergrades with sub-type (a). The basic difference is that those thickened cells close to the mucilage cells are much more radially elongated than the other; the result is a distinct secondary rim on either side of the seed (Fig. 4, K-L; 5, B). Moreover, the walls of most of the thickened cells are convoluted. In some cases the mucilage cells only form a swollen rim, e.g., *G. amplexans*, whilst in others they form a more or less distinct wing, and the mucilage cells tend to overlie the thickened cells, e.g., *G. stelligera*, *G. calcarata*.

In still others the mucilage-cells appear to be non-functional and collapse before maturity, e.g., *G. macmillanii* (Fig. 5, A).

Type 3. (a)

Embryo slightly spathulate, $a : b = 2 : 2\frac{1}{2}$ or $2 : 3$. Intergrades with both types 2 and 4. They tend to be more rectangular in cross-section and the result is that the thickened cells towards the margin are much more radially elongated than the other thickened cells and they tend to overlie the mucilage cells somewhat. Moreover, the mucilage-cells are usually collapsed in the mature condition, giving a 3-rimmed structure to the margin, e.g., *G. heterophylla*, *G. hispida*, *G. disperma*, *G. auriculata* and *G. koningsbergeri* (Fig. 5, D-I). The mucilage cells appear to be non-functional. In all of these except *G. heterophylla* the integument cells between the vascular bundle and the endosperm have heavily thickened walls (cf. *Calogyne*). In *G. koningsbergeri* the mucilage cells are very reduced in number and the epidermis consists almost entirely of thickened cells (Fig. 5, F).

Type 3. (b)

Embryo slightly spathulate, $a : b = 2 : 3$ to $2 : 2\frac{1}{2}$. The marginal thickened cells here are very curved and appear crescent shaped in section, giving a secondary rim to the margin of mucilage cells, e.g., *G. hederacea*, *G. boormanii*, *G. sepalosa*. In *G. sepalosa* the marginal integument cells are heavily thickened (Fig. 5, C, J).

Type 4

Embryo spathulate, $a : b = 2 : 3$ to $2 : 4$. Intergrades to some extent with type 2b. The thickened cells have much-convoluted walls and those towards the margin are very elongated, far from overarched the mucilage-cells;

however, these latter overlie the thickened cells to a considerable degree. The mucilage cells are numerous and in all cases form a fairly distinct wing. Mucilage appears to be present in all the wings of type 4 seeds. The embryo tends to be spatulate and the cotyledons are generally slightly displaced laterally and do not directly overlay each other, e.g., *G. heteromera*, *G. glauca*, *G. subintegra*, *G. pinnatifida* (Fig. 6, A).

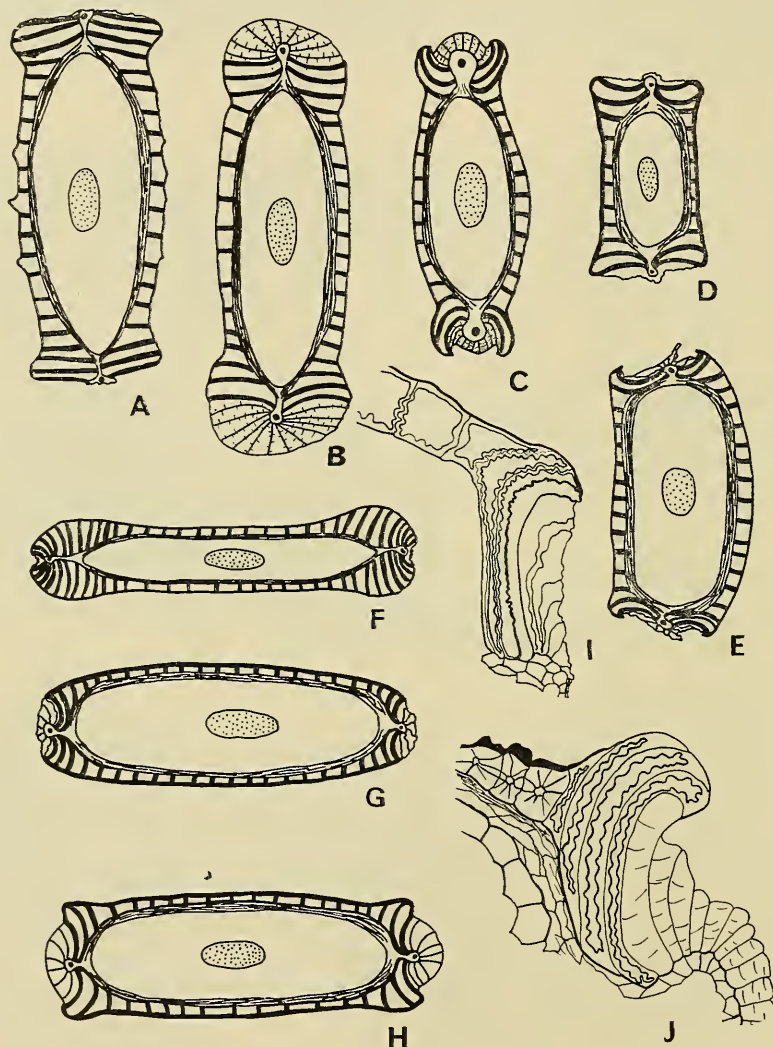


Fig. 5. Transverse sections of seeds. A. *G. macmillanii* $\times 20$; B. *G. amplexans* $\times 20$; C. *G. hederacea* $\times 20$; E. *G. heterophylla* $\times 20$; F. *G. koningsbergeri* $\times 20$; G. *G. hispida* $\times 20$; H. *G. lanata* $\times 20$; I. *G. heterophylla*, marginal epidermis $\times 160$; J. *G. boormannii*, marginal epidermis $\times 160$.

Type 5

Embryo spatulate, $a : b = 2 : 3$. This type shows distinct similarities with the previous one. The mucilage cells overlie the marginal thickened cells but those not overlying are not elongated radially. Moreover, the wing is a massive structure, as thick as the body of the seed throughout its width, because the internal parenchyma is very well developed, e.g., *G. mitchellii* (Fig. 6, B).

Type 6

The extreme form of this, type *b*, is represented by *G. havilandii* var. *pauperata* and *G. concinna*. The mucilage cells overlie the thickened cells as a separate, free flap; the cell lying immediately upon the thickened epidermis

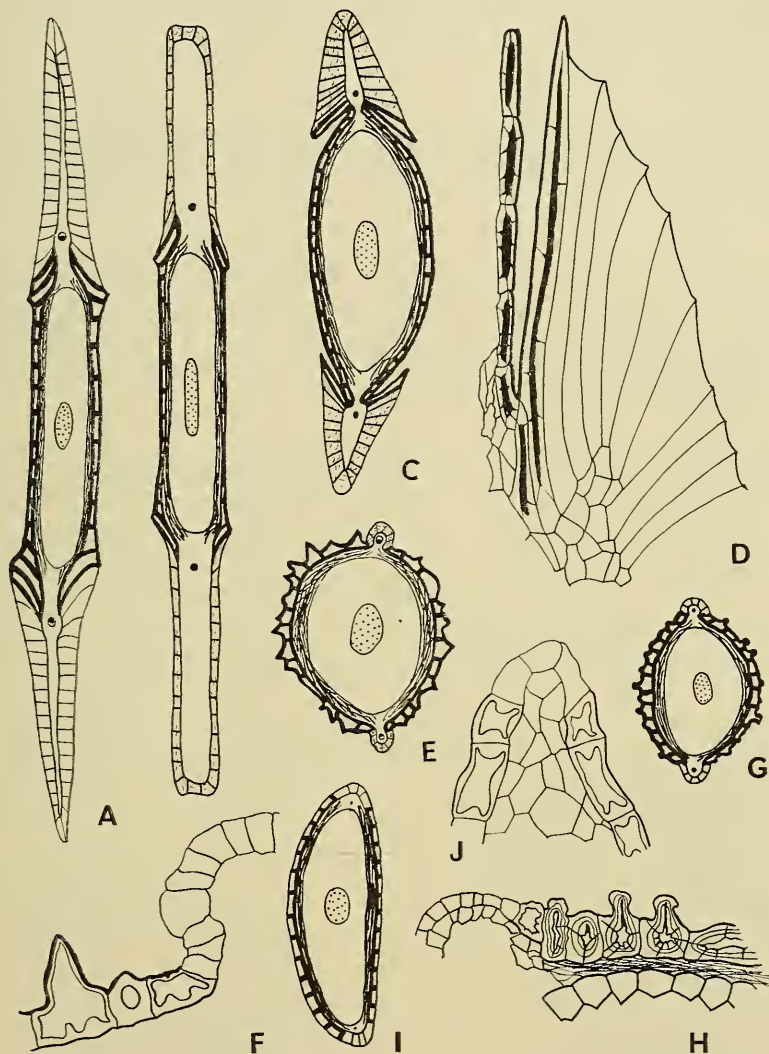


Fig. 6. Transverse sections of seeds. A. *G. linifolia* $\times 20$; B. *G. mitchellii* $\times 40$; C. *G. havilandii* var. *pauperata* $\times 20$; D. *G. havilandii* var. *pauperata*, marginal epidermal cells $\times 160$; E. *Pentaptilon careyi* $\times 20$; F. *P. careyi*, marginal epidermal cells $\times 160$; G. *Catosperma goodeniacearum* $\times 20$; H. *C. goodeniacearum* marginal epidermal cells $\times 160$; I. *G. pumilio* $\times 20$; J. *G. pumilio* marginal epidermal cells $\times 160$.

(but free from it) is thickened and spicule-like, but apparently not mucilaginous. The thickened cells of the testa are rather narrower and thinner-walled than in the previous types and the walls are less convoluted (Fig. 6, C, D).

G. caerulea and *G. pterygosperma* represent type 6a, a form closer to that found in type 2 in that the overlapping is much less pronounced (Fig. 7, J, K).

Type 7

Embryo \pm terete, $a:b=1:1$. In this type the cell walls of the epidermis, even of the "thickened" cells, remain quite thin; the form of the marginal "mucilage" cells is no different from the thickened cells except in the thinner cell walls; this paler rim is almost invisible as there are so few mucilage cells. Indeed, it is even doubtful whether these latter actually contain mucilage, e.g., *G. pumilio* (Fig. 6, I, J).

CALOGYNE

Two types of seed are found in this genus, which are directly comparable with types also found in *Goodenia*. These types are numbered below as in the latter genus.

Type 4

All *Calogyne*s with a 3-fid style have this seed type with mucilage cells \pm collapsed at maturity, e.g., *C. pilosa*, *C. purpurea* (Fig. 8, A, B). They resemble the *G. hispida* group of *Goodenia* spp. in that the integument cells between the vascular bundle and the endosperm have thickened cell-walls. Embryo slightly spatulate, $a:b=2:3$.

Type 6

Calogyne berardiana, with a 2-fid style, has this seed type which is quite distinct from type 4 (Fig. 7, A). Embryo spatulate; $a:b=2:4$.

TABLE 1
Seed types in Goodenia and related genera (see Fig. 10)
(Sections and Series according to Krause, 1912)

	Section	Series
TYPE 1		
<i>G. barbata</i> R. Br.	Eu-goodenia	Suffruticosae
<i>G. strophiolata</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. chisholmii</i> Maiden		
<i>G. phyllicoides</i> F. Muell.	Monochila	
TYPE 2. a		
<i>G. ovata</i> Sm.	Eu-goodenia	Suffruticosae
<i>G. varia</i> R. Br.	Eu-goodenia	Suffruticosae
<i>G. laevis</i> Benth.	Eu-goodenia	Suffruticosae
<i>G. viscida</i> R. Br.	Monochila	
<i>G. eatoniana</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. azurea</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. ramellii</i> F. Muell.	Eu-goodenia	Racemosae
<i>G. stapfiana</i> Krause	Eu-goodenia	Racemosae
<i>G. scaevolina</i> F. Muell.	Eu-goodenia	Caeruleae
<i>G. paniculata</i> R. Br.	Amphichila	
b		
<i>Neogoodenia minutiflora</i> Gard. et George ..		
<i>G. scapigera</i> R. Br.	Monochila	
<i>G. quadrilocularis</i> R. Br.	Eu-goodenia	
<i>G. stelligera</i> R. Br.	Eu-goodenia	Racemosae
<i>G. dimorpha</i> Maiden et Bêche		
<i>G. decurrens</i> R. Br.	Eu-goodenia	Racemosae
<i>G. bellidifolia</i> R. Br.	Eu-goodenia	Racemosae
<i>G. amplexans</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. glabra</i> R. Br.	Eu-goodenia	Rosulatae
<i>G. grandiflora</i> Sims	Eu-goodenia	Foliosae
<i>G. macmillanii</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. calcarata</i> F. Muell.	Eu-goodenia	Foliosae

TABLE 1.—Continued.

Seed types in *Goodenia* and related genera (see Fig. 10)
(Sections and Series according to Krause, 1912)

	Section	Series
TYPE 3		
<i>G. disperma</i> F. Muell.	Eu-goodenia	Suffruticosae
<i>G. rotundifolia</i> R. Br.	Eu-goodenia	Rosulatae
<i>G. affinis</i> De Vr.	Eu-goodenia	Rosulatae
<i>G. hederacea</i> Sm.	Eu-goodenia	Rosulatae
<i>G. boormanii</i> Krause	Eu-goodenia	Rosulatae
<i>G. heterophylla</i> Sm.	Eu-goodenia	Rosulatae
<i>G. sepalosa</i> F. Muell. ex Benth.	Eu-goodenia	Foliosae
<i>G. hispida</i> R. Br.	Eu-goodenia	Foliosae
<i>G. auriculata</i> Benth.	Eu-goodenia	Foliosae
<i>G. armstrongiana</i> De Vr.	Eu-goodenia	Foliosae
<i>G. koningsbergeri</i> (Back.) Back. ex Bold.		
<i>Calogyne pilosa</i> R. Br.		
TYPE 4		
<i>G. glauca</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. heteromera</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. microptera</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. forestii</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. pusilliflora</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. heterochila</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. vilmoriniae</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. tenuiloba</i> F. Muell.	<i>Incertae sedis</i>	
<i>G. corynocarpa</i> F. Muell.	Eu-goodenia	Foliosae
<i>G. armittiana</i> F. Muell.	Eu-goodenia	Pedicellosae
<i>G. pinnatifida</i> Schlecht.	Eu-goodenia	Pedicellosae
<i>Calogyne berardiana</i> (Gaudich.) F. Muell.		
TYPE 5		
<i>G. mitchellii</i> Benth.	Eu-goodenia	Foliosae
TYPE 6. a		
<i>G. havilandii</i> var <i>pauperata</i> Black		
<i>G. micrantha</i> Helms ex Christ. et Ost.		
<i>G. concinna</i> Benth.	Eu-goodenia	Pedicellosae
b		
<i>G. trichophylla</i> De Vr.	Eu-goodenia	Caeruleae
<i>G. pterygosperma</i> De Vr.	Eu-goodenia	Caeruleae
<i>G. incana</i> R. Br.	Eu-goodenia	Caeruleae
<i>G. caerulea</i> R. Br.	Eu-goodenia	Caeruleae
<i>Symphlobasis macroplectra</i> (F. Muell.) Krause		
TYPE 7		
<i>G. pumila</i> R. Br.	Amphichila	
TYPE 8 = Type 7 of <i>Scaevola</i> (which see)		
<i>Verreauxia reindwardtii</i>		

SELLIERA

The fruit of this genus is berry-like but the seed is equatable with type 3 in *Goodenia*. Embryo slightly spatulate; $a:b=2:3$.

Indeed, it shows a striking resemblance to that of *G. koningsbergeri* although somewhat smaller. The mucilage is extremely sticky and probably is important in distribution as the "berry" appears to be eaten by sea-birds which thereby pick up these seeds on parts of their body, e.g., *Selliera radicans*.

It has only been possible to examine immature seeds of *S. exigua*, but it seems highly improbable that they are at all similar to those of *S. radicans*.

VELLEIA

Embryo spatulate; $a:b=2:4$ to $2:5$. Here again the basic form of the seed is very similar to a type within *Goodenia*, i.e., type 4, with a fairly conspicuous wing. The mucilaginous cells, however, pass on directly from the thickened ones; these are not curved as in the *Goodenia* type although

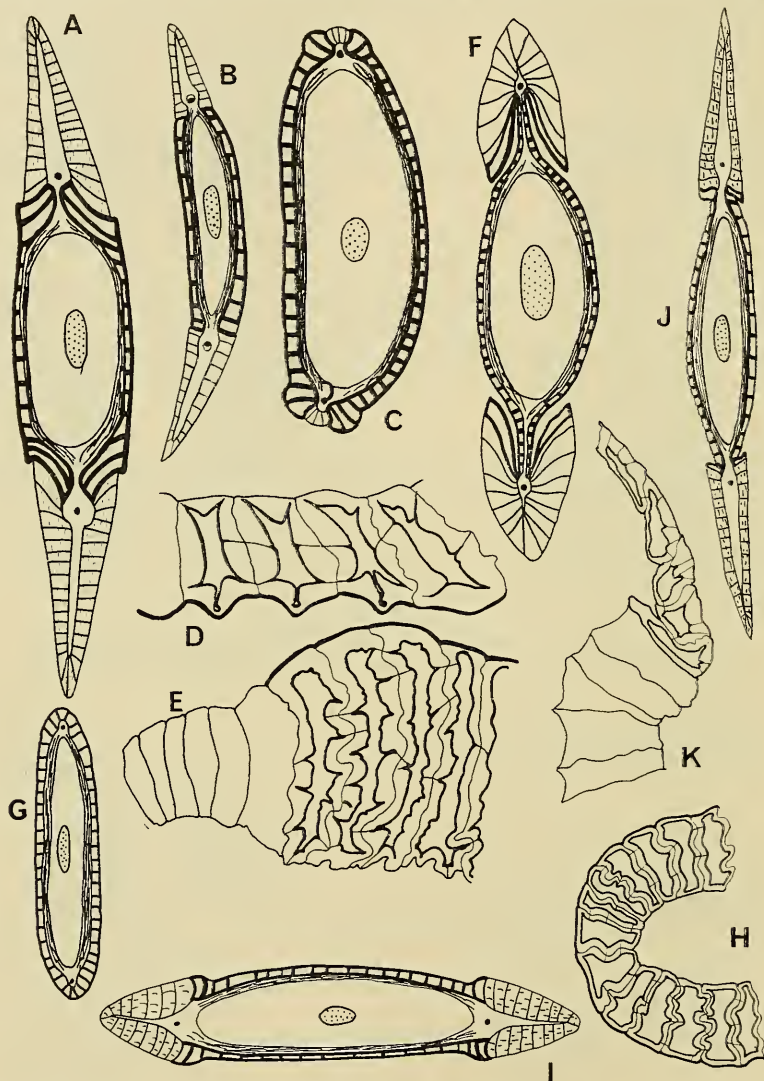


Fig. 7. Transverse sections of seeds. A. *Calogyne berardiana* $\times 50$; B. *Velleia spathulata* $\times 10$; C. *V. montana* $\times 20$; D. *V. montana*, epidermal cells $\times 160$; E. *V. montana*, marginal epidermal cells $\times 160$; F. *Goodenia concinna* $\times 12$; G. *Verreauxia reinwardtii* $\times 20$; H. *V. reinwardtii* marginal epidermal cells; I. *Neogoodenia minutiflora* $\times 20$; J. *Goodenia pterygosperma* $\times 20$; K. *G. pterygosperma*, marginal epidermal cells $\times 160$.

the walls are very convoluted. In only one of the species examined, *V. montana*, is there any conspicuous departure from this type. In *V. montana* the mucilage cells are very much reduced in number and form a minute rim enclosed by the overarching marginal thickened cells, e.g., *V. spathulata*, *V. paradoxa*, *V. discophora*, *V. cynopotamica* (Fig. 7. B-E).

CATOSPERMA

Embryo almost terete. In this genus the fruit is hard and indehiscent and contains up to four seeds. Each seed shows clearly the differentiation into thickened cells and "mucilage" cells, although the walls of the former are not convoluted as in *Goodenia*, etc., and the mucilage-cells, although very thin-walled, do not apparently contain mucilage. The marginal thickened cells are no different from their fellows and the mucilage cells form a rounded rim. The embryo appears to be \pm terete e.g. *C. goodeniacearum* (Fig. 6, C-H).

PENTAPTILON

This genus again shows an indehiscent dry fruit. The 4-6 seeds are pendulous and otherwise are remarkably similar to those of *Catosperma* (Fig. 6, E, F). Embryo not observed.

VERREAUXIA

Embryo almost terete. Another genus with indehiscent fruits, this time, however, containing only one seed. The fruit has an outer layer of thin-walled, collapsed cells, whilst the inner layer, probably corresponding to the true ovary wall, has interlocking cells with thickened walls. The seed does not correspond to any of the *Goodenia* types listed above. In *V. reinwardtii* the epidermis is undifferentiated, all the cells have thickened walls and there are no mucilage cells, but the seed is compressed and has no strophiole (cf. *Goodenia* type 1) (Fig. 7, E, H). There is only a single vascular strand which passes from the funicle around the periphery of the seed and reaches almost to the micropyle; the embryo was not observed.

In *V. paniculata* the situation is very slightly different in that the marginal cells do show some difference from the immediately adjacent cells. The walls are quite straight and not thickened so much, whereas the adjacent cells on the seed face are convoluted. Moreover, the walls of the marginal cells tend to stain more deeply with Chlorazol Black. These marginal cells do not, however, appear to contain mucilage, e.g., *V. reinwardtii*, *V. paniculata*.

SYMPHIOBASIS

No mature seed of this genus was available for study.

NEOGOODENIA

Embryo spathulate; $a:b=2:3$. This genus is distinguished from *Goodenia* primarily upon the single seed borne in a thin-walled, indehiscent, unilocular fruit (Gardner and George, 1963). The fruit wall appears to be quite unthickened (cf. *Verreauxia*, *Dampiera* and *Scaevola*) and the seed closely resembles that of some *Goodenia* spp. The epidermal cells on the body of the fruit have somewhat thickened walls and those of the prominent rim contain considerable quantities of mucilage. The marginal thickened cells do not project so extensively into the interior of the seed and the vascular bundle is consequently not "pinched off" from the rest of the integument (Fig. 7, I). Otherwise the seed falls close to *Goodenia* type 2b. The cotyledons are narrow. The fruit is actually similar to *Verreauxia* in that the seed is inserted on a basal abortive septum.

SCAEVOLA (see Fig. 11)

The seed of all *Scaevola* species show a single vascular bundle, unbranched, which extends from the funicle right around the seed almost to the micropyle. The seed is frequently slightly compressed and the vascular bundle runs just beneath the more or less prominent, marginal ridge (Fig. 3, C).

The fruit of *Scaevola* is indehiscent with a varying development of hard 'endocarp' towards the locules. This 'endocarp' grades into the unthickened cells towards the outside; there is no clear demarcation line as in *Dampiera stricta*. The testa of the seed consists of thin-walled cells which, at maturity, show bands of thickening; the cells are all of the same type; there are no

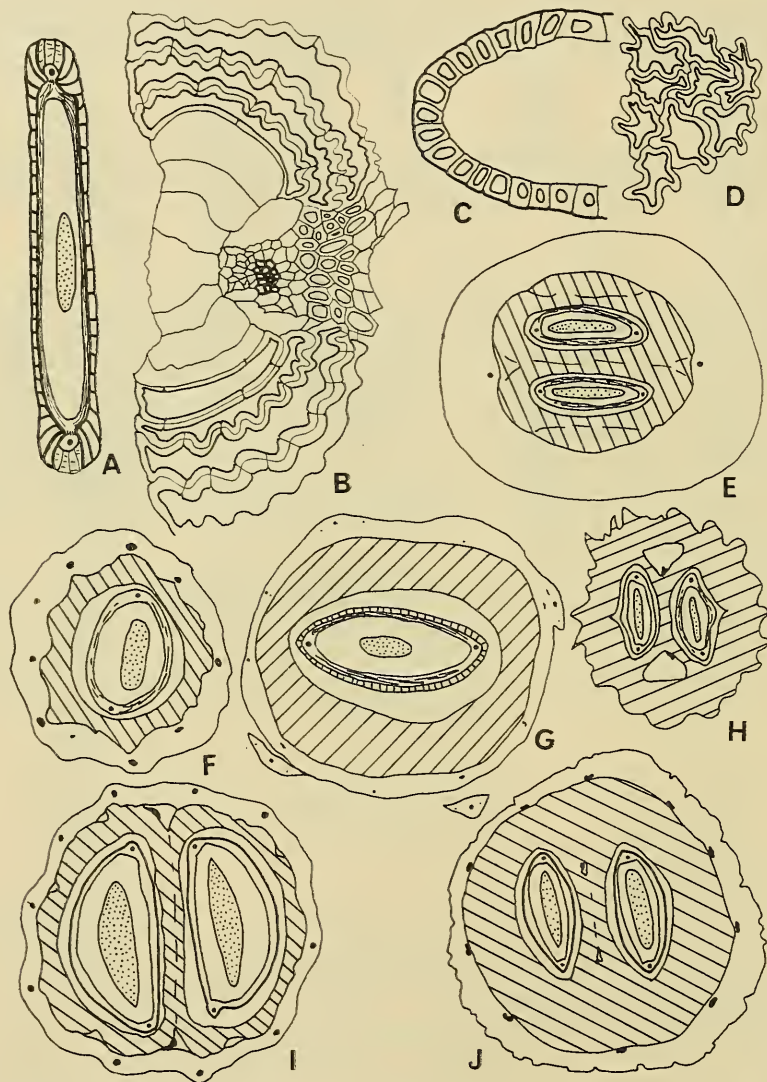


Fig. 8. Transverse sections of seed. A. *Calogyne pilosa* $\times 12$; B. *C. pilosa*, marginal epidermal cells $\times 160$; C. *Scaevola stenophylla*, marginal epidermal cells; D. surface view of epidermal cells, *S. stenophylla*. Transverse sections of fruits. E. *Scaevola spinescens* $\times 4$; F. *Scaevola humifusa* $\times 8$; G. *S. helmsii* $\times 20$; H. *S. calendulacea* (pyrene only); I. *S. ramosissima* $\times 8$; J. *S. chamissoniana* $\times 4$.

mucilage cells as in *Goodenia*. This applies to all the species except *Scaevola stenophylla*, *S. helmsii* and *S. fasciculata*: here, although there is no differentiation into mucilage cells towards the margin, the epidermal cells are all distinctly and more or less uniformly thickened. Moreover, they show the sinuate outline, in surface view, found in *Goodenia*, not the more regular shape as in other

Scaevola sp. Three zones are distinguished in pseudo-fruit walls and they will be referred to as epicarp, mesocarp and endocarp, although they do not correspond exactly to the zones so named in the true drupe. The epicarp here, in fact, is probably derived from the outer floral whorls (in the phylogenetic sense) whilst both the mesocarp and endocarp develop from tissue which is probably derived from the ovary itself. All three zones consist of more than one layer of cells and, as defined here, either the epicarp or the mesocarp may contribute towards the succulent part of the false-fruit where such occurs. The seven types of fruit described below are based upon differences in the constitution of these three layers and the number of loculi. Since much of the work was conducted upon herbarium material, it was not always possible to determine the relative succulence of the various layers. In the lists “*” indicates where fresh material has been examined.

Type 1.—Four loculi present; mesocarp and endocarp not differentiated from each other, epicarp dry.

S. porocarya. The fruit of this species contains four seeds which each occupy a separate loculus; two of these loculi arise at a lower level than the other two. In addition to these fertile loculi there are a large number of irregular cavities which apparently arise through the disintegration of vascular bundles. Bentham (1863) states that only two seeds are present but, although this may be the case when only two ovules are fertilized, the general rule is that four seeds are formed. There is no distinct separation of the pseudo-fruit wall into a fleshy external layer and a hard “endocarp”; the external tissues are only slightly softer than the internal ones (Fig. 9, H).

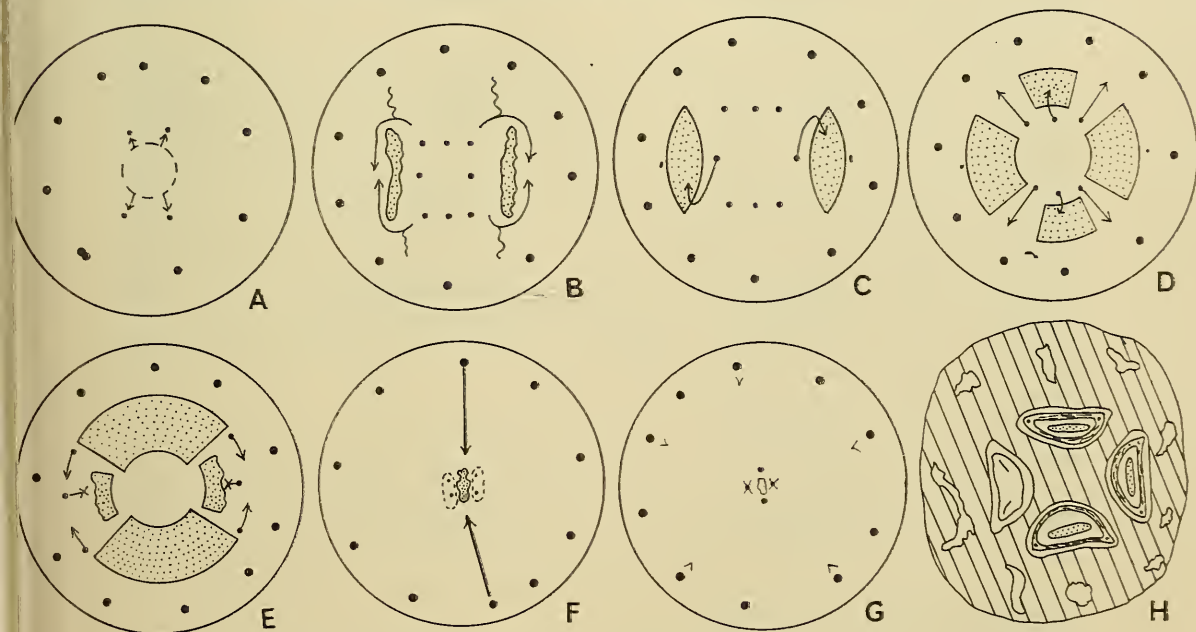


Fig. 9. *Scaevola porocarya*. A-G. Diagrams to show the vascular pattern at different levels in the pseudo-ovary. A. near base; B. two lowermost loculi appearing, movement of strands to form carpel dorsal shown; C. strands entering lower ovules; D. strands entering upper ovules; E. dorsals of lateral carpels disappear (x) replaced by laterals (shown by arrows); F. dorsals of anterior and posterior carpels pass to base of style; G. laterals of lateral carpels disappear (x) and staminal strands begin to separate from sepal-radius bundles (Δ); H. Transverse section of fruit showing spaces in “endocarp”.

This is the only case, so far reported in the family, in which a 4-locular ovary has been seen (cf. Carolin, 1958). It therefore calls for a rather more detailed consideration of the vascular network of the flower. This is shown in the series of diagrams which have been compounded from serial sections prepared in the manner indicated in the previous paper (Carolin, 1959). At the base of the flower the stele resolves into 7-10 peripheral bundles, mostly on petal or sepal radii (eventually 10 are formed) with a ring of indeterminate bundles in the centre. These very soon give rise to four bundles which pass outwards and around the back of the two lower loculi which are just forming; there they fuse and form a single bundle which eventually ends blindly at the base of the style. Meanwhile the central ring has resolved into light bundles; four of these pass into the ovules, the other four pass outwards (carpel laterals) and eventually appear to end blindly at the base of the style. Two large bundles are formed anteriorly and posteriorly, both from bundles on petal radii, which pass inwards and up into the style unchanged. The derivation of the other bundles to the floral parts is the same as in other *Scaevola* spp. (Carolin, 1959), and the full interpretation of the positioning of the different organ bundles is shown in Fig. 9, A-G.

Type 2.—2-loculi, sometimes with sterile loculi, mesocarp and endocarp not differentiated from each other, epicarp various.

This type would seem to be a straightforward derivation from type 1 by abortion of the lateral loculi. The pseudo-carpel lateral bundles (Carolin, 1959) are included within the hard endocarp and the epicarp shows varying degrees of succulence. Some species have no sterile lateral loculi, e.g., *S. oppositifolia*, *S. nitida*.

However, although *S. porocarya* is the only species which is known to have a truly 4-locular ovary, a number of others have false, sterile loculi in addition to those containing the ovules. In *S. calendulacea* (Fig. 8, H) and *S. globulifera*, for example, the cells surrounding the pseudo-carpel lateral bundles remain parenchymatous as the endocarp is formed by the thickening of the walls of the other innerzone cells. At maturity these parenchymatous cells have broken down, probably due to their failure to grow at the same rate as the others, and a large cavity remains. These two lateral cavities are connected at the base of the septum by a single cavity formed by the disintegration of the axile vascular strands and the parenchymatous tissue surrounding them (cf. *S. porocarya*). In *S. attenuata* the single basal cavity is extremely well marked, whilst the pseudo-carpel laterals extend only for a very short distance up the ovary so that no lateral cavities are formed.

The situation appears to be directly comparable to that in the Hawaiian *S. cerasifolia* (Skottsberg, 1923). Moreover, despite Skottsberg's illustrations to the contrary, *S. chamissoniana* also has very minute sterile loculi alternating with the two fertile loculi (Fig. 8, J). The former represent the ruptured pseudo-carpel lateral bundles; none of the adjacent tissues remain unthickened.

The epicarp may be dry as in *S. globulifera* or very well developed and succulent as in *S. calendulacea*.

The endocarp may be differentiated in colour and thickness of the cell walls from those of the inner endocarp as in *S. nitida*, *S. saligna*. In this species the inner endocarp is brown and the outer zone is colourless; moreover, the pseudo-carpel lateral bundles occur very close to the outer margin of the mesocarp. In this particular species no false loculi occur. The thickness of the mesocarp is often not uniform giving a gibbous appearance to the fruit of some species, e.g., *S. dielsii*.

Type 3.—2-loculi usually with 2 sterile loculi in a non-succulent mesocarp differentiated from the endocarp; epicarp various.

In this type the inner zone is not uniform, but two layers which intergrade into each other are formed. In *S. taccada* this inner endocarp consists of cells with thickened walls whilst the outer mesocarp has suberized cell walls.

TABLE 2
Fruit types in Scaevola (see Fig. 11)
(Sections according to Krause, 1912)

	Section
TYPE 1	
<i>S. porocarya</i> F. Muell.*	Xerocarpaea
TYPE 2 (without sterile lateral loculi)	
<i>S. oppositifolia</i> Roxb.	Enantiophyllum
<i>S. saligna</i> Forst. f.*	Xerocarpaea
<i>S. nitida</i> R. Br.*	Xerocarpaea
<i>S. dielsii</i> E. Pritzel*	Xerocarpaea
<i>S. attenuata</i> R. Br.	Xerocarpaea
(with sterile lateral loculi)	
<i>S. calendulacea</i> (Kennedy) Druce*	Xerocarpaea
<i>S. globulifera</i> Labill.*	Xerocarpaea
<i>S. chamissoniana</i> Gaudich.	Sarcocarpaea
<i>S. micrantha</i> Presl.	Sarcocarpaea
<i>S. indigofera</i> Schlechter	Sarcocarpaea
<i>S. glandulifera</i> DC.	Xerocarpaea
TYPE 3 (with a distinct mesocarp containing the lateral bundles.)	
<i>S. taccada</i> Roxb.	Sarcocarpaea
<i>S. mollis</i> Hook. et Arn.	Sarcocarpaea
TYPE 4	
<i>S. spinescens</i> R. Br.*	Crossotoma
<i>S. tomentosa</i> Gaudich.*	Crossotoma
TYPE 5	
<i>S. ovalifolia</i> R. Br.*	Xerocarpaea
<i>S. hookeri</i> F. Muell.*	Pogonanthera
<i>S. crassifolia</i> Labill.*	Xerocarpaea
<i>S. ramosissima</i> (Sm.) Krause	Xerocarpaea
TYPE 6	
<i>S. humifusa</i> De Vries	Xerocarpaea
<i>S. albida</i> (Sm.) Druce	Xerocarpaea
TYPE 7 (8 of <i>Goodenia</i>)	
<i>S. stenophylla</i> (F. Muell.) Benth.	Xerocarpaea
<i>S. fasciculata</i> Benth.	Xerocarpaea
<i>S. helmsii</i> E. Pritzel	Xerocarpaea

Embedded in the mesocarp are the two, narrow false-loculi formed in the same way as those of type 3. *S. mollis* has much the same construction, but the false-loculi are considerably larger in size (Skottsberg, 1923).

Type 4.—2-loculi, no sterile loculi; mesocarp succulent.

This represents the condition where only the innermost zone is thickened and the pseudo-carpel lateral bundles are embedded in a succulent mesocarp-epicarp, e.g., *S. tomentosa* (Fig. 8, E).

Type 5.—2-loculi; usually with 2 (small) sterile loculi; epicarp and mesocarp dry.

This seems to be the commonest form of fruit found in the sect. *Xerocarpacea*. It can, in fact, be interpreted in two ways: either as the change of the mesocarp surrounding the pseudo-carpel laterals into the collapsed, thin-walled condition of the epicarp, or as the movement, outwards, of the pseudo-carpel laterals into the epicarp. The tissues surrounding these bundles tend to disintegrate to form small false-loculi just on the innermost boundary of the epicarp, e.g., *S. ramosissima* (Fig. 8, I), *S. crassula*.

Type 6.—1-loculus; \pm small sterile loculi; epicarp and mesocarp dry.

This differs from the previous type only in that the septum between the two ovules is present only at the base of the ovary (cf. Carolin, 1959), e.g., *S. albida*, *S. humifusa* (Fig. 8, F).

Type 7 (8 of *Goodenia*).

The pseudo-lateral carpel bundles in this case are included within the endocarp. There is no tendency to form sterile "loculi" and, due to the septum being extremely short, the fruit appears to be unilocular. The epicarp is very thin and, unlike most of the representatives of type 7, the endocarp surface is smooth, not rugose. The seeds are quite different from all the other *Scaevola* species in the very much thickened testa cell-walls and the irregular surface outline of these same cells (Fig. 8, G, C, D). In this respect they resemble the seeds of *Verreauxia* and, somewhat, those of *Goodenia scapigera*.

DISCUSSION

The genera of the Goodeniaceae can be divided into two groups on the basis of the seed vascular supply, corresponding precisely with that grouping suggested previously by Carolin (1959) and Peacock (1961). In the *Dampiera* group, i.e. *Dampiera*, *Anthotium*, *Leschenaultia* and *Brunonia*, the seeds have either a double vascular supply or a single strand; neither system, however, reaches right around to the micropylar side, they gradually get smaller and usually disappear towards the top of the seed. *Dampiera* spp. are fairly consistent in showing a double supply, in sect. *Camptospora* much elaborated to supply the large, peculiarly shaped seed. In *Brunonia* a single strand is found reaching around the top of the seed, whilst in *Leschenaultia* and *Anthotium* the single strand is very short indeed. The short, single strand can probably be interpreted as due to the fusion of the double supply of *Dampiera*.

So far as the fruits are concerned, *Anthotium* has the only dehiscent fruit in the group and the seeds are the only ones in the group with a conspicuously thickened testa epidermis. In *Dampiera* and *Leschenaultia* the seeds are contained in "endocarps", which function as the protective covering, the thickening of the seed coat epidermis is reduced to a few lignin bands per cell in *Dampiera* and is virtually non-existent in *Leschenaultia*. In *Brunonia* the protection is supplied by the tough calyx-tube whilst both the fruit wall and the seed-coat are very thin. The "endocarp" of *Dampiera* and *Leschenaultia* appears to correspond to the true fruit wall whilst the outer, unthickened parts correspond to the united, outer floral whorls (cf. Carolin, 1959). Whilst the general structure of the pseudo-fruit of *Dampiera* sect. *Dicoelia* does not differ greatly from that of *Scaevola* sect. *Xerocarpacea*, the seed vasculature is totally different. There would appear to be no phylogenetic connection.

Thus it appears that, although this group is a fairly well-defined unit, one cannot detect any consistent and correlated trends within it. If we accept that the multiple nature of the strand is more primitive than a single strand, we are left with *Anthotium* with a primitive, capsular fruit and an advanced,

reduced seed vasculature, *Dampiera* with a primitive seed vasculature and an advanced indehiscent fruit, and *Leschenaultia* with an advanced seed vasculature and formation of an "endocarp" but a primitive (numerous) number of seeds. *Brunonia* shows so many other differences that it is impossible to fit it into any series at all. It seems, then, that this group represents the ends of a number of diverging evolutionary lines, each branch of which has had an effectively separate history, not basically uniform as in the other group.

The other group consists of *Goodenia*, *Calogyne*, *Selliera*, *Pentaptilon*, *Catosperma*, *Neogoodenia*, *Verreauxia Velleia*, *Scaevola*, *Diaspasis*.

If we accept as a general, although not binding rule, that the capsule is more primitive than an indehiscent fruit and a seed with a uniform testa is more primitive than one in which the seed coat is differentiated into several cell-types, the group of species centred around *Goodenia barbata* appear to carry the most primitive features in this group. It is interesting to note that the seeds are also strophiolate. It appears improbable that they are particularly close to the ancestral form, since the basic chromosome number is different from the rest of the group (Peacock, 1961). The latter author has listed other differences from the rest of the genus *Goodenia* and it seems they may merit separate generic rank. All other species of *Goodenia*, *Calogyne*, *Selliera*, *Pentaptilon*, *Catosperma*, *Neogoodenia* and *Velleia* have more or less flattened seeds with at least some of the cells on the margin differentiated into thin-walled "mucilage" cells. From this point of view, the last seven may be considered as "satellite" genera around the large, somewhat, polymorphic genus *Goodenia* (Fig. 10). Of the various seed-types (except type 1) described under *Goodenia* it is rather difficult to decide which, if any, is the most primitive. Type 2 would seem to be the least differentiated, particularly the form found in *G. ovata* where the marginal thickened cells are scarcely differentiated from the outer thickened cells. But, as will be suggested later, it is possible that there has been a reversal in that some forms have reverted to an entirely undifferentiated testa epidermis. It is difficult to say for certain whether the form of *G. ovata* seeds is due to primitiveness or more or less advanced reduction. However, the shrubby habit, the anatomy and the inflorescence (cf. Krause, 1912) indicate that the species associated with *G. ovata* have a combination of what are generally considered to be primitive characters and it seems reasonable to accept the *G. ovata* form as a starting point. Further evolution has progressed mainly through the elaboration of the marginal thickened cells and changes in the number and arrangement of the "mucilage" cells. Type 2 (*b*) represents a line in which the marginal thickened cells have become much enlarged, but the arrangement of them and their relationships with the "mucilage" cells remains much the same as in the *G. ovata* group.

Type 3 represents the line in which the marginal thickened cells are enlarged and overarching the mucilage cells which are often very reduced in number and, frequently, apparently non-functional. In *G. koningsbergeri*, in particular, the number of mucilage cells is very small. It is usual, in these cases in particular, to find that the integument cells immediately in from the vascular bundle become thickened, presumably to seal off the inner parts of the seed more effectively than the thin-walled "mucilage" cells, in this case probably containing little if any mucilage. In addition to this trend of reduction in the mucilage cell number, another trend seems to be operating in those species assigned to type 3 (*b*). In this case the marginal thickened cells become curved above, thus giving a ridge marking off the mucilage-cells from the body of the seed. The superficial appearance is not unlike that found in type 2 (*b*) but is due to an entirely different configuration of the cells involved (Fig. 10).

Another line is represented by those species assigned to type 4. In this case the marginal thickened cells are elongated, but their long axis is placed so that they underlie many of the "mucilage" cells.

Type 5 represents a derivative of this line in which the horizontal axis of the "mucilage" cells is shortened and the parenchymatous part of the wing is fairly massive.

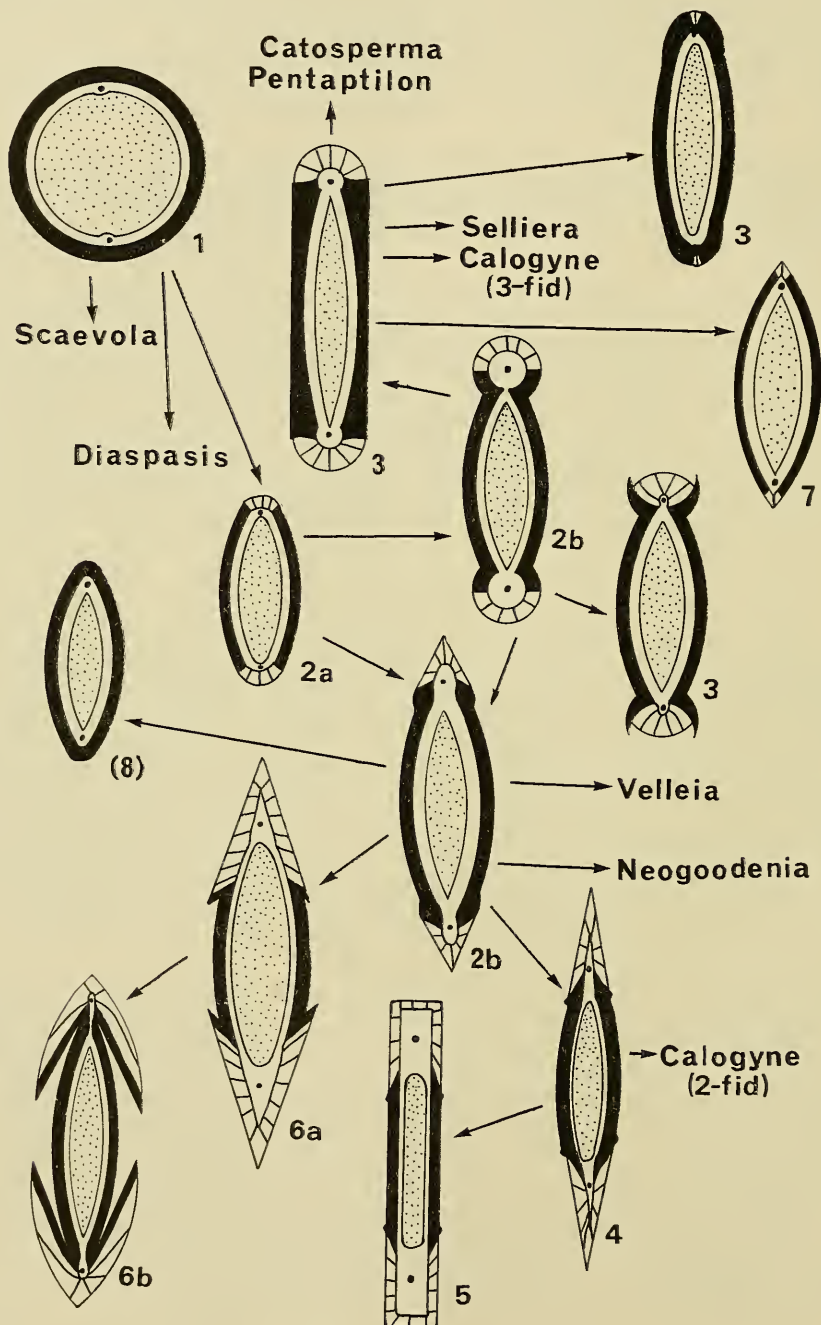


Fig. 10. Diagram to show the suggested relationships of the types of seed found in *Goodenia* and its satellite genera. Hatched areas=mucilage cells; solid black areas=thickened epidermal cells; stippled areas=endosperm and embryo.

Yet another line is shown by type 6, in which one of the marginal thickened cells becomes much elongated and supports the large "mucilage" cells overlying the outer parts of the body of the seed. These peculiarities are relatively undeveloped in *G. pterygosperma* and *G. trichophylla* but extremely well developed in *G. micrantha*.

Type 7 is a very reduced form and it is difficult to fit it into any of these lines; it could be the end product of reduction of any of them. Without evidence from other characters, which is being accumulated, it is impossible to place this species in any series.

These lines all seem to converge on that of type 2 (*a*) and, to some extent, intergrade with it. This is further evidence for considering it to be the basic, primitive type. Despite these intergrades the types are fairly distinct and close-knit and, for this reason, represent real biological units. Evidence is being accumulated that other distinctive characters are correlated with them. This being so it would appear that Krause's sections and series (1912) require a drastic overhaul. Of his sections, *Monochila* is particularly unsatisfactory, since it contains some species having type 2 and one species with type 1 seeds. *G. barbata*, *G. strophiolata* (and *G. chisholmii*), from section *Eugoodenia* should be linked with *G. phyllicoides*. Ser. *Suffruticosae* seems to be a rather heterogeneous group and needs breaking up. Ser. *Caeruleae* divides quite neatly into two groups with type 2 and type 6 seeds respectively. Ser. *Racemosae* is fairly uniformly type 3. Ser. *Foliosae*, on the other hand, splits into three fairly well defined groups: those centred around *G. grandiflora* with type 2 (*b*), those around *G. hispida* with type 3, and those around *G. heterochila* with types 4 and 5. There seems little doubt that this is a heterogeneous taxon when such widely differing seed types are found within it. It is interesting to find that *G. grandiflora* frequently has bracteoles despite Krause's placing them in the *Ebracteolatae*. Indeed, the presence or absence of bracteoles seems to be of little value in itself.

To turn to the "satellite" genera. *Calogyne* again has shown its heterogeneous nature (see Carolin, 1959). *C. berardiana* belongs to the evolutionary line represented by *G. glauca* and *G. heterochila*. All the other species belong to the line represented by *G. hispida* and *G. koningsbergeri*. *Calogyne*, as constituted, is an unsatisfactory genus and the 2-fid-styled species should be separated from those having 3-fid styles. *Selliera* belongs to the evolutionary line of type 3 similar to *G. koningsbergeri* which, indeed, has been referred to *Selliera* in the past.

Neogoodenia has a rather more basic seed-type, and it is consequently rather more difficult to assign it to any particular line of development. Although there is only a single seed in an indehiscent fruit, there is no doubt of its close affinity with *Goodenia* on account of its seed type. All the "satellite" genera so far discussed are so close to *Goodenia* that a case could be made for their inclusion in that genus.

The seeds of *Velleia* are very similar to types 3(*b*) and 2(*b*) of *Goodenia*. Thus, although they possess the "mucilage" cells, and thus a differentiated seed coat, the type shown is a fairly basic one. It seems probable, then, that *Velleia* has separated from the bulk of *Goodenia* subsequent to the differentiation of the mucilage cells in phylogenetic history, and thus after both had diverged from the *G. barbata* group: a further argument for accepting the latter as a separate genus. *Velleia*, however, must remain a generic entity by virtue of its other characters.

Both *Catosperma* and *Pentaptilon* show a seed structure undoubtedly derived from a *Goodenia* type, but the reduction which has apparently accompanied the closure of the fruit has made it impossible to decide to which line they belong on this evidence.

Verreauxia differs from all the other genera examined in this group so far by its lack of mucilage cells. All the epidermal cells of the compressed seed, even those on the margins, are uniformly thickened. They are distinctly thickened and the vasculature is quite definitely of the *Goodenia* type—there is no doubt about the position of the genus in this group. Thus *Verreauxia* is either a case of extreme reduction, the possibility of which is shown by *Goodenia koningsbergeri*, or has retained the primitive condition also shown by the *G. barbata* group. Evidence from other directions is needed before this problem can be resolved.

The discovery of the 4-locular nature of the ovary of *Scaevola porocarya* is of some significance in that it forces a new interpretation of the ovary structure, at least of *Scaevola*. Figures 9, A–G, show that the loculi must be considered as carpels; they have a vasculature in fair agreement with this hypothesis, although those of the opposing pairs of carpels have reacted in different ways to the adnation of the outer whorls to the ovary. The lateral pair of carpels have a dorsal strand each, produced from the union of two strands, themselves derived separately from the central stele. This is a very unusual condition; although the double nature of the dorsal bundle has been established in some primitive groups it is unexpected here. The posterior-anterior pair have a dorsal vasculature exactly similar to that found in other *Scaevola* spp. (Carolin, 1959). The adjacent lateral bundles of the carpels are united and the laterally opposite pairs eventually unite. Neither these nor the dorsal bundles of the lateral carpels extend into the style, rather unusual, as in other species the former do so and in *S. ramosissima* all four lateral bundles separate and are persistent through the style (Carolin, 1959). It appears that the evolution of the vascular system of the flower is just as uneven as the larger differences found in the *Dampiera* group (see above), advanced and primitive conditions occurring in the same species, indeed, at different levels within the same flower. It seems, then, that *Scaevola* has had a rather different history from that of the rest of the *Goodenia* group. The behaviour of the “pseudo-carpellary dorsal” bundles at the top of the ovary of *Goodenia*, etc., implies that the loculus is derived from two carpels (Carolin, 1959). The bundles similarly positioned in *Scaevola* remain single always; this fact, together with the discovery of the structure of *S. porocarya*, implies that the loculus in the case of *Scaevola* represents a single carpel. Furthermore, if this reasoning is accepted, *Goodenia* has “true” carpels placed diagonally in the flower whilst *Scaevola* has them placed anterior-posteriorly and (sometimes) laterally. This is not necessarily a particularly far-reaching difference since these two conditions may occur elsewhere in the plant kingdom within the same species (e.g., *Campanula*). It does, however, imply that the evolutionary histories of *Scaevola* and *Goodenia* are separate, and similarities in the ovary structure are the result of convergence rather than common origin.

The seeds of *Scaevola* are usually more or less compressed, although the structure of the testa is rather similar to that of *Dampiera*. However, there is little doubt that it is not closely allied to *Dampiera* since the seed has a single strand, the floral structure is different (Carolin, 1959) and the chromosome number is different (Peacock, 1961).

Within the genus the fruit types (see Fig. 11), once again, show only incomplete correlation with the Sections proposed by Krause. After the type exhibited by *S. porocarya*, it seems reasonable to suppose that type 2 is the most primitive since, in this case, the tissues which are most probably gynoecial in origin behave as a unit, i.e., form the “endocarp”. The false-loculi really represent a case of “regressive convergence” towards the condition in type 1 subsequent to the loss of the lateral carpel (loculi). These taxa belong mostly to the *Sarcocarpaea* and all of them have a highly developed “mesocarp”, be it fleshy or corky. The trend in the Sections *Crossotoma*, *Xerocarpaea* and *Pogonanthera* is towards the exclusion of part of the tissue of gynoecial origin

from "endocarp" formation, this part being around the false-loculi caused by the disruption of the "lateral" bundles. In sect. *Crossotoma* no false-loculi are formed and these tissues are included in the fleshy "mesocarp"; in sects *Xerocarpaea* and *Pogonanthra* the false-loculi are frequently present and the "mesocarp" is thin. *S. crassifolia* and *S. nitida* resemble *S. porocarya*

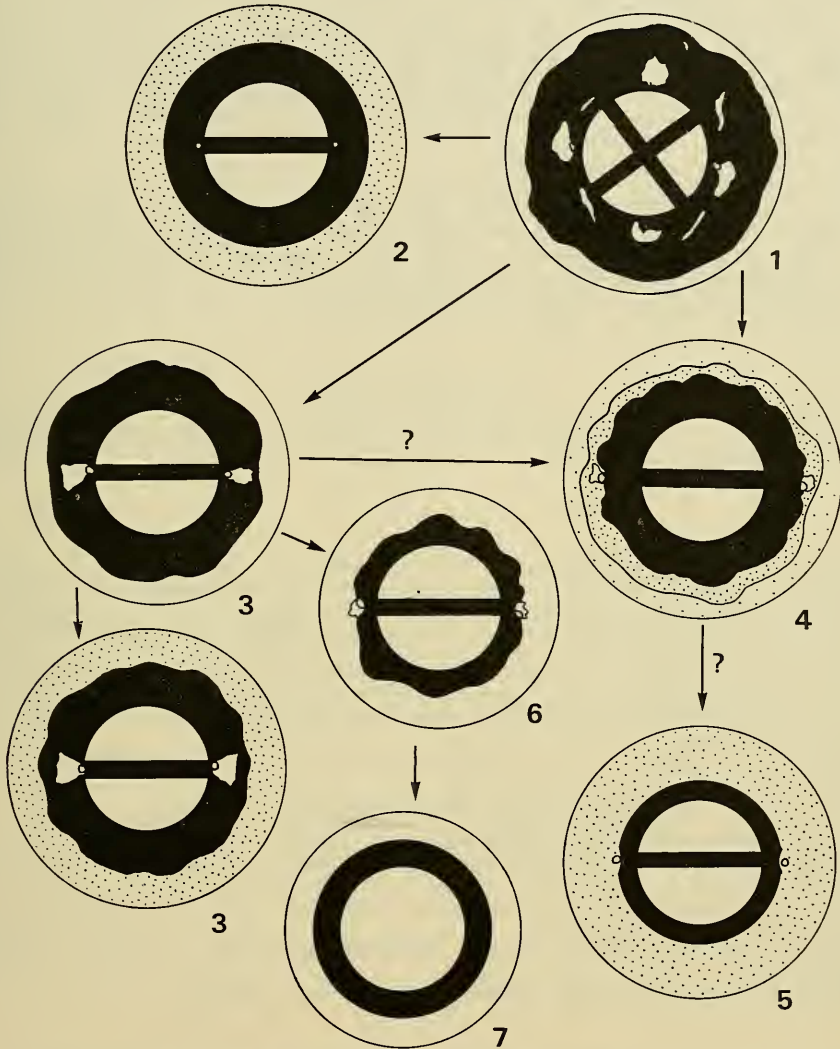


Fig. 11. Diagram to show the suggested relationships of the pseudo-fruit types of *Scaevola*. Open areas=dry, soft tissue; solid black areas=dry, hard tissue; stippled areas=fleshy (or corky) tissue.

so closely in many respects there seems little doubt that they are related despite the first two species having type 2 fruits. It appears, then, that the *Sarcocarpaea* have originated from the 4-locular type separately from the *Xerocarpaea* group and possibly earlier. Sect. *Pogonanthra* shows very few differences from *Xerocarpaea* in fruit structure and sect. *Crossotoma* appears to be a fleshy-"mesocarp" derivative of the *Xerocarpaea*.

The three species, *S. stenophylla*, *S. helmsii*, *S. fasciculata*, show very real differences in the seed form from the rest of genus; they also had a significantly different floral construction (Carolin, 1959). In fact, the seeds have very definitely thickened epidermal cells, quite unlike the lignin banding seen in the rest of *Scaevola* spp. Indeed, they resemble those of *Verreauxia* or *Goodenia* without the marginal mucilage cells. It was previously suggested that these species were closer to *Verreauxia* than *Scaevola* (Carolin, 1959) but other characters would seem to link them with a group of *Goodenia* spp., centred around *G. scapigera*. This would, in fact, imply not only an evolutionary trend towards reduction in ovule number and closure of the fruit, but also a loss of the mucilage cells and a reversal, in the evolutionary sense, to something more closely resembling the *G. barbata* type. The seed of *S. helmsii*, however, is compressed and not \pm circular in transection.

The rest of *Scaevola* ser. *Uniloculatae* shows a straightforward unilocular drupaceous fruit with a thin "mesocarp" and no false-loculi. Although there is no indication from the fruit or seed that there have been several origins of the unilocular condition from the (apparently) bilocular condition (cf. Carolin, 1959), other characters indicate that this may be so.

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Voucher Specimens

Leschenaultia biloba Carolin 3428 (Syd.). *L. divaricata* Carolin 43 (Syd.). *L. filiformis* Perry 1710 (Canb.). *L. linarioides* Carolin 3324 (Syd.). *L. longiloba* no voucher. *Anthotium rubriflorum* no voucher. *Dampiera coronata* Carolin 3243 (Syd.). *D. purpurea* Carolin 4439 (Syd.). *D. stricta* Peacock 6011.26.6 (Syd.). *D. trigona* Carolin 3055 (Syd.). *Diaspasis filiformis* no voucher.

Goodenia affinis Carolin 3340 (Syd.). *G. amplexans* Black, Burnside Road 2.1904 (N.S.W.). *G. armstrongiana* Chippendale 18.5.59 (N.S.W. ex N.T. 6199). *G. armitiana* Perry 1904 (Canb.). *G. auriculata* Perry 1772 (Canb.). *G. azurea* Chippendale 12.4.59 (N.S.W. ex N.T. 5659). *G. barbata* Peacock 6012.5.1 (Syd.). *G. bellidifolia* Carolin 565 (Syd.). *G. caerulea* Sargent 4069 (N.S.W.). *G. boormanii* Peacock 6111.26.1 (Syd.). *G. calcarata* Beadle 8.1941 (Syd.). *G. chisholmii* Peacock 6012.4.1 (Syd.). *G. concinna* Benn 4.10.1963 (Syd.). *G. corynocarpa* no voucher. *G. decurrens* Peacock 6011.26.3 (Syd.). *G. dimorpha* Carolin Oct. 1963 (Syd.). *G. disperma* Mueller, Burnett River (K.). *G. eatoniana* Koch, 2032 (N.S.W.). *G. glabra* Peacock

6111.31.1 (Syd.). *G. glauca* Wharton 9.2.1952 (Syd.). *G. grandiflora* Cambage 3978 (Syd.). *G. havilandii* var. *pauperata* Specht and Carrodus 34 (Syd.). *G. hederacea* Carolin 2044 (Syd.). *G. heterochila* Perry 2405 (Canb.). *G. heterophylla* Carolin 2032 (Syd.). *G. hispida* Eddy, 23.3.58 (N.S.W. ex N.T. 5220). *G. incana* Cleland, Nargin, 11.08 (N.S.W.). *G. koningsbergeri* no voucher. *G. laevis* Carolin 3583 (Syd.). *G. macmillanii* Lucas, Macalister River, 12.10 (N.S.W.). *G. micrantha* Peacock 60856.5 (Syd.). *G. microptera* Chippendale 2.5.58 (N.S.W. ex N.T. 4232). *G. mitchellii* Carolin 4055 (Syd.). *G. ovata* Carolin 1936 (Syd.). *G. paniculata* Peacock 6012.2.2 (Syd.). *G. phyllicoides* Carolin 3575 (Syd.). *G. pinnatifida* Peacock 6111.9.1 (Syd.). *G. pterygosperma* Benn 8.10.1963 (Syd.). *G. pumilio* McKee 9471 (N.S.W.). *G. pusilliflora* Whaite 2491 (N.S.W.). *G. quadrilocularis* no voucher. *G. ramellii* Perry 1918 (Canb.). *G. rotundifolia* Peacock 6012.6.3 (Syd.). *G. scaevolina* Perry and Lizarides 2296 (Canb.). *G. scapigera* Carolin 3556 (Syd.). *G. sepulosa* Perry 1708 (Canb.). *G. stelligera* Peacock 6012.12.1 (Syd.). *G. strophiolata* Doodlakine, Fitzgerald Nov. 1903 (N.S.W.). *G. tenuiloba* Peacock 60865.1 (Syd.). *G. trichophylla* Pritzel 827 (N.S.W.). *G. varia* Maiden Kangarcalaw 1902 (N.S.W.). *G. viscida* no voucher. *G. vilmorinae* Perry and Lazarides 2225 (N.S.W.).

Selliera radicans Peacock Jan. 1958 (Syd.). *Calogyne pilosa* Specht 218 (Canb.). *C. berardiana* Carolin 4224 (Syd.). *Neogoodenia minutiflora* George 910 (Perth). *Symphobasis macropectra* Speck 1368 (N.S.W.). *Pentaptilon careyi* Carolin 3325 (Syd.). *Verreauxia reinwardtii* Peacock 60845.1 (Syd.). *V. paniculata* no voucher. *Catosperma goodenicearum* Chippendale 14.7.1956 (N.S.W. ex N.T. 2331). *Scaevola albida* Carolin 2082 (Syd.). *S. calendulacea* Carolin 0785 (Syd.). *S. chamissoniana* Smith-White, Aug. 1961 (Syd.). *S. crassifolia* Carolin 3373 (Syd.). *S. dielsii* Briggs (N.S.W. 52429). *S. fasciculata* Briggs (N.S.W. 52427). *S. glandulifera* Peacock 60876.1 (Syd.). *S. globulifera* Briggs 3.10.1960 (Syd.). *S. helmsii* Carolin 3134 (Syd.). *S. hookeri* Carolin Jan. 1957 (Syd.). *S. humifusa* Carolin 3538 (Syd.). *S. indigofera* McKee 4714 (Syd.). *S. micrantha* McKee 4279 (Syd.). *S. mollis* Smith-White, Aug. 1961 (Syd.). *S. nitida* Carolin 3190 (Syd.). *S. ovalifolia* Carolin 4270 (Syd.). *S. oppositifolia* no voucher. *S. porocarya* Carolin 3358 (Syd.). *S. ramosissima* Carolin 3653 (Syd.). *S. spinescens* Carolin 3074 (Syd.). *S. taccada* S.U. Biol. Soc. Jan. 1948 (Syd.). *S. tomentosa* Carolin 3323 (Syd.).